Evolutionary Patterns in Fossil Lineages

Gene Hunt
Department of Paleobiology
National Museum of Natural History
Smithsonian Institution
Two Paradigms

Phyletic Gradualism

Punctuated Equilibria

Eldredge & Gould (1972)
Disputed Interpretations

- Same data interpreted in conflicting ways
- Inadequacy of verbal models
- Led to incompatible summaries of the subject

Gingerich (1976)
Evolution in Fossil Lineages

I. Fitting Statistical (not Verbal) Models

II. Applications
   1. Evolutionary Modes
   2. Tempo
   3. Punctuations
   4. Process Models
Evolutionary Modes

- Methods proposed to sort out different modes of evolution (e.g., Raup 1977, Bookstein 1987, Gingerich 1992, Roopnarine 2001)
- Generally rely on Random Walk as a null model
General Random Walk

Phenotype

Evolutionary “steps”

Step mean ($\mu_s$) = **directionality**
Step variance ($\sigma^2_s$) = **volatility**
General Random Walk

Evolutionary "steps"

step mean ($\mu_s$) = **directionality**
step variance ($\sigma^2_s$) = **volatility**
Modeling Stasis

- Simple white noise (Sheets & Mitchell 2001)
- Optimum at $\theta$, with variance of $\omega$
Statistical Inference

- Expected change in phenotype is normally distributed, with mean and variance determined by model parameters & age model.
- Allows calculation of likelihood = $\text{Pr}[\text{data} \mid \text{model}]$.
- Maximizing likelihoods gives best parameter estimates.
Models of Evolution

Directional change

Random walk

Stasis

2 parameters

1 parameter

2 parameters
Comparing Models

- Models differ in complexity (# parameters)
- More parameters → higher log-likelihood
- \( AIC = -2\log(L) + 2K \)
- Bias-corrected form, \( AICc \), is better
- Akaike weights represent relative support among models
Advantages

- There is no null model
- Powerful and flexible machinery
- Sampling error is correctly handled
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Evolutionary Modes

Gradualism dominates

Levinton (2001)
Gingerich (1985)

Erwin & Antsey (1995)

Gould (2002)
Jablonski (2000)
Jackson & Cheetham (1999)

Stasis/Punc. dominates

Directional change

Random walk

Stasis
Data

• 251 time-series from 53 lineages
• 6 - 114 samples per time-series

**Planktonic Microfossils**
- foraminifera [23]
- radiolaria [9]
- conodonts [9]

**Benthic Microfossils**
- foraminifera [37]
- ostracodes [60]

**Macrofossils**
- mollusks [70]
- trilobites [1]
- mammals [40]
- fish [2]
Relative Importance of Evolutionary Modes

- Gradualism dominates
  - Levinton (2001)
  - Gingerich (1985)
- Random walk
  - Erwin & Antsey (1995)
- Stasis/Punctuated Equilibrium dominates
  - Jablonski (2000)
  - Jackson & Cheetham (1999)

- Directional change: 5%
- Random walk: 49%
- Stasis: 46%
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Rates of Evolution

Parameter of the Random Walk (step variance) is useful as a rate metric:

1. uncorrelated with interval length for true random walks
2. known range of values under drift (Lynch 1990)
3. can be measured from A-D or phylogeny
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Does improved fit of punctuated models outweigh their greater complexity?

• General form:
  stasis - change - stasis

• Class of models in which evolutionary dynamics shift over time

Malmgren et al. (1983)
Two kinds of punctuations

Unsampled

Sampled

5 parameters

8 parameters

Use $\text{AIC}_c$ scores to weigh model support
• Cisne et al. (1980) documented pulsed change in trilobite *Flexicalymene*

• Levinton (2001) cited it as an example of gradual change

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<table>
<thead>
<tr>
<th>model</th>
<th>segments</th>
<th># par</th>
<th>AICc</th>
<th>weight</th>
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<tbody>
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<td>Random Walk</td>
<td>1</td>
<td>1</td>
<td>8.01</td>
<td>0.375</td>
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<tr>
<td>Directional</td>
<td>1</td>
<td>2</td>
<td>10.31</td>
<td>0.119</td>
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<tr>
<td>Stasis</td>
<td>1</td>
<td>2</td>
<td>49.48</td>
<td>0.000</td>
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<tr>
<td>I Punctuation</td>
<td>2</td>
<td>4</td>
<td>7.42</td>
<td>0.505</td>
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</table>
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Other Kinds of Models

Process-based models

1. Causal drivers (e.g., Temperature tracking)
2. Adaptive evolution
Selection in Fossil Lineages

- Originally, Directional mode thought to be indicative of natural selection
- Rareness of clearly Directional was disconcerting
- Best test case: stickleback from varved lakes (Bell et al. 2006)
What should adaptive evolution look like?

**Scenario:** Environment shifts, population is dislocated from an adaptive peak.
Adaptive (OU) Model

**Four key parameters**

- starting phenotype
- optimal phenotype
- strength of selection
- step variance (drift)
Bell’s stickleback

- ~5,000 stickleback fish from diatomite mine
- Countable yearly varves
- Resolution = 250 yrs
- Counted dorsal spines, pterygiophores, scored pelvis
- Independent evidence for selection for reduced armor

Numerous tests failed to find selection (directionality)
Re-analysis

- Fit adaptive (OU), and neutral drift (Random walk) models
- Adaptive models conclusively beat neutral ones ($w > 0.99$)

Implications

• Consistency check: all models imply reasonable $N_e$

<table>
<thead>
<tr>
<th>trait</th>
<th>$N_e$</th>
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<tr>
<td>dorsal spines</td>
<td>575 – 4,023</td>
</tr>
<tr>
<td>pelvic score</td>
<td>889 – 6,222</td>
</tr>
<tr>
<td>pterygiophores</td>
<td>851 – 5,957</td>
</tr>
</tbody>
</table>

• Weak selection: fitness differences $\approx 1$ - $5\%$ or less

• With coarser resolution, this would look like unsampled punctuation
Conclusions I

1. Banish the word ‘gradual.’ Evolution can be:
   - directional or not
   - homogeneous or heterogeneous

2. Directional evolution is rarely observed

3. Heterogeneous dynamics are not uncommon

4. Skeletal reduction in sticklebacks was adaptive
Conclusions II

There are many advantages to formulating evolutionary interpretations as statistical models:

• unambiguous model comparisons

• parameters are evolutionary informative (rates, directionality, natural selection)
Acknowledgments

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